Perspectives in Plant Ecology, Evolution and Systematics 16 (2014) 143–153

Contents lists available at ScienceDirect

Perspectives in Plant Ecology, Evolution and Systematics

journal homepage: www.elsevier.com/locate/ppees

Research article

Can livestock grazing maintain landscape diversity and stability in an ecosystem that evolved with wild herbivores?

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ARTICLE INFO

Article history:
Received 8 August 2013
Received in revised form 15 April 2014
Accepted 22 April 2014
Available online 5 May 2014

Keywords:
Physiognomy
Soil erosion
Stocking rate
Tussock grasslands
Vegetation changes
Woodlands

ABSTRACT

The livestock industry is converting mountain ecosystems in central Argentina into rocky deserts. However, it helps to conserve plant biodiversity, presumably because the ecosystem has evolved under wild herbivores now locally extinct. We hypothesized that low or moderate livestock stocking rates, instead of the high stocking rates currently used for commercial production, might mimic pre-hispanic herbivore pressures. Thus, the mosaic of physiognomies necessary to maintain landscape diversity and soil integrity could be preserved. To test this hypothesis we tracked physiognomic changes in 200 plots (16 m^2 each) under different stocking rates, including livestock exclusion, for five years. Contrary to our expectations, we found that both low and moderate stocking rates failed to maintain landscape diversity. As observed for livestock exclusion, low to moderate stocking rates promote retraction and, finally, elimination of short grazing lawns and their replacement by tall tussock grasslands, or possibly by woody vegetation. In turn, heavy grazing pressure maintains the desired short lawn patches in the landscape, but also promotes a concomitant loss and eventual elimination of woodlands, together with an expansion of bare rock as a consequence of soil erosion. These results indicate that the present mosaic of physiognomic types is difficult to maintain and raise questions about the past stability of the ecosystem. We suggest that during the last 400 years of livestock production in the ecosystem, short lawns have been maintained by means of heavy stocking rates and anthropogenic fires ignited to eliminate tussocks. However, this relative stability of lawns has been attained concomitantly with a progressive loss of soils and woodland area. We also discuss some possible explanations for the maintenance of short lawns before the introduction of livestock, based on main climatic and floristic shifts during the late Holocene.
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Introduction

Livestock grazing may be necessary to maintain rangeland ecosystem structure and function when native wild herbivore populations are decimated or extinct, or if livestock presence is ancient in the ecosystem (Perevolotsky and Seligman, 1998; Cingolani et al., 2005a, 2008a). In productive grasslands, the absence of grazing disturbance can lead to the dominance of a few large and competitive plant species, reducing alpha diversity (Milchunas et al., 1988; Osem et al., 2002; Cingolani et al., 2005a, 2008a; Altesor et al., 2006). Additionally, the accumulation of standing and dead biomass may alter fire regimes in undesired ways (Hobbs et al., 1991). Conversely, intense trampling by livestock, uneven animal distribution and excessive plant consumption can produce irreversible ecosystem degradation, even in productive ecosystems (Mwendera et al., 1997; Cingolani et al., 2005a, 2008a). If not evolved under heavy grazing of large herbivores, productive ecosystems may collapse under livestock maintained at commercially optimal stocking rates (Diamond, 2005; Cingolani et al., 2005a, 2008a; Lunt et al., 2007). In such cases, native plant diversity might only benefit from light livestock grazing, i.e. with densities well below the commercial optimum (Milchunas et al., 1988; Cingolani et al., 2005a).

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http://dx.doi.org/10.1016/j.ppees.2014.04.002
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The upper belt of Córdoba Mountains (Argentina), in southern South America, is a productive ecosystem composed of a mosaic of tall grasslands, short lawns, woodland patches and rocky areas (Cingolani et al., 2003, 2004). Contrasting evidence complicate the classification of this ecosystem as having "long" or "short" evolutionary history of grazing (*sensu* Milchunas et al., 1988). On the one hand, this area was continuously occupied by large herbivores since geological times (Díaz et al., 1994). After the extinction of Pleistocene mega-herbivores about 10 000 years ago, the ecosystem sustained populations of wild middle-sized herbivores, such as camelids (*Lama guanicoe*) and deer (*Ozotoceros bezoarticus*), until their local extinction at the beginning of the 20th century (Medina, 2006; Medina and Rivero, 2007). Additionally, it was suggested that local inhabitants raised domestic camelids (*Lama glama*) in the area before the European settlement; and finally, domestic European livestock were introduced in these mountains, about 400 years ago (Díaz et al., 1994). In line with this background, the rapid loss of alpha diversity in grassland communities when livestock are excluded supports the idea that vegetation is adapted to herbivory (Díaz et al., 1994; Pucheta et al., 1998a; Cingolani et al., 2003, 2010). The tolerant response of most grazed plants, including the dominant tree *Polylepis australis* Bitter, provided further support for this hypothesis (Díaz et al., 2001; Cingolani et al., 2007; Giorgis et al., 2010). On the other hand, alternative evidence challenges the idea of a long evolutionary history of heavy grazing. Archaeological studies indicate that populations of wild camelids declined progressively in the area during the Holocene, as human populations grew and hunting pressure increased (Medina and Rivero, 2007). Additionally, Medina et al. (2007, cited in Pastor et al., 2012) analyzed bone remains and did not find convincing evidence of pre-hispanic rise of domestic camelids. These records suggest that the introduction of European domestic livestock represented a rapid increase in grazing pressure, generating a novel impact on the system. In agreement with the latter view, we have observed that livestock introduction has triggered soil erosion processes, still active, which are driving the system into a rocky desert (Cingolani et al., 2008b; Cáceres, 2009; Cingolani et al., 2013). Moreover, heavy consumption of *P. australis* by livestock seems to have contributed to woodland retraction, despite tolerant response of this species to moderate browsing levels (Teich et al., 2005; Renison et al., 2006; Cingolani et al., 2008b; Giorgis et al., 2010).

Since these findings reveal negative effects on ecosystem properties driven either by livestock exclusion or by high stocking rates, we surmised that the system is adapted to low or moderate grazing pressure, but not to the high grazing pressures exerted by livestock in large portions of the area (Cingolani et al., 2008b). Therefore, we hypothesized that low or moderate livestock grazing pressures can mimic the pre-hispanic herbivore grazing, preserving the mosaic of physiognomic types necessary to sustain landscape plant diversity and wildlife (Cingolani et al., 2008a, 2010). We tested this hypothesis by tracking physiognomic changes under different livestock grazing pressures for five years. This was facilitated by the creation of a National Park, where livestock were maintained or re-introduced in some areas, with different management schemes, while excluded in others (APN, 2007). In the present contribution we aim to analyze how livestock stocking rate and timing of grazing influence changes in plant physiognomy. We predict that (1) grazing exclusion will produce an expansion of woody plants and tussock grasses, and a retraction of bare rock and short lawn-forming plants; (2) low or moderate stocking rates will prevent directional physiognomical changes, i.e. will maintain a stable mosaic; and (3) high stocking rates will produce an expansion of lawn-forming short plants and bare rock, along with a retraction of woody plants and tussock grasses. In our analysis, we also considered the influence of site and landscape physical properties on physiognomic changes.

Methods

Study area

The study was conducted in the upper belt of Córdoba mountains (1700–2800 m a.s.l.), in part of the Quebrada del Condorito National Park and surrounding private properties (Córdoba Province, Argentina, Fig. 1). At 2200 m a.s.l. mean temperatures of the coldest and warmest months are 5.0 and 11.4 °C, respectively, with no frost-free period. Mean annual precipitation is 900 mm, mostly concentrated in the warmest months, from October to April (Cabido, 1985; Colladon et al., 2010). During the study period (2004–2009), hydrologic year rainfall (September to August) was similar to or lower than the long term average (908, 901, 771, 834 and 868 mm, from the first to the last study year, respectively, Colladon et al., 2010). The landscape is a mosaic of woodlands, grasslands, rocky outcrops and erosion stone-lands. Woodlands are generally small patches dominated by *P. australis*. Grasslands can be dominated by tall tussock grasses, such as *Poa stuckertii* (Hack.) Parodi, *Deyeuxia hieronymi* (Hack.) Türpe and *Festuca* spp., or by forbs and short graminoids (i.e., short grasses, sedges and rushes) in which case they are called "grazing lawns" (*sensu* McNaughton, 1984). Rocky outcrops have variable levels of plant cover, including all life-forms, whereas erosion stone-lands are always scarcely vegetated (Cingolani et al., 2004). Most species within the local flora are characteristic of this upper mountain belt and a good number of them are endemics (Cabido et al., 1998). In some portions of the National Park, livestock were maintained or re-introduced in an attempt to prevent loss of plant diversity and excessive biomass accumulation, which can trigger wildfires (APN, 2007). Different livestock management schemes have been implemented, involving variable stocking rates and timing of grazing (Table 1, Fig. 1). In the surrounding, privately owned areas stocking rates are generally higher than inside the National Park, and fire is often used to reduce tussock cover and stimulate regrowth. These private properties are part of National and Provincial Reserves, which were created as buffer areas for the National Park, but few effective conservation actions have been taken in these areas.

Sampling design and field measures

In September 2004 we established 142 permanent plots (4 m × 4 m). In September 2005 and 2006 we added 40 and 18 plots, respectively, totalling 200. We distributed the plots in fenced paddocks or areas limited by natural boundaries (hereafter named "paddocks" for simplicity), with variable stocking rates and timing of grazing (Fig. 1, Table 1). Plots were representative of paddocks' vegetation and topography, except that we did not select tall closed woodlands or sites completely dominated by rock or in very steep slopes. At the initial date some plots contained two or more physiognomies (e.g. short lawn and tussock grassland). The land-use history up to the start of our study was not homogeneous across paddocks. Within the National Park, most paddocks under livestock grazing were the result of approximately five years of the same management practice. The age of exclosures at the initial date, both within and outside the National Park, varied between two and five years. In turn, plots under livestock grazing located outside the National Park had a longer and uninterrupted history of livestock grazing, which is more difficult to track.

At plot set up, we measured slope aspect (degrees from the North), slope inclination (%) and soil depth (cm). We also

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